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The Impact of Hybrid Vigour on Commercial Traits of the Indian Tropical Tasar Silkworm, *Antheraea mylitta* Drury (Lepidoptera: Saturniidae)

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The bivoltine tropical tasar ecoraces of *Antheraea mylitta* Drury produces cocoons for seed production under seed crop rearing (July-August with 22~30°C temperature and 50~70% relative humidity) and for silk production under commercial crop rearing (September-December with 17~27°C temperature and 60~80% relative humidity). To consider the impact of hybrid vigour on egg, larva, cocoon and silk related commercial traits, the F_1 hybrids made among Daba, Jata and Raily ecoraces were assessed successively for three years. The hybrid vigour in the F_1 hybrid of Daba × Jata (T_7) was positive for egg fertility (+23.1%), shell weight (+25.6%), silk yield (+79.0%) and filament length (+68.1%), with filament of high denier (11.98d) and reduced larval span (–7.1%). The Jata × Daba (T_8) hybrid has shown negative heterosis in egg fertility (–8.0%) compared to the other F_1 hybrids, Daba × Raily (T_9) and Raily × Daba (T_{10}), when they rise simultaneously during the commercial crop season. The better performance of parental ecoraces (T_4 to T_6) in their commercial traits during commercial crop over parents of seed crop (T_1 to T_3) and the superior performance of F_1 hybrids (T_7 to T_{10}) over parents of commercial crop (T_4 to T_6) during commercial crop season indicates the apparent hybrid vigour in tasar F_1 hybrids. As the Daba × Jata (T_7) and Jata × Daba (T_8) F_1 hybrids have shown highest hybrid vigour, their rearing during commercial crop can optimize the silk productivity and commercial sustenance of the tasar silk industry.

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Introduction

The tasar (vanya) silk is produced by the wild sericigenous and polyphagous *Antheraea mylitta* Drury (Lepidoptera: Saturniidae), distributed all along central India (12 ~ 31°N latitude and 72 ~ 96°E longitude). Though the species has a rich genetic resource with forty four ecoraces (Suryanarayana and Srivastava, 2005; Reddy, 2010) only the Daba and Sukinda races are semi-domesticated and applied for commercial rearings and their hybrid vigour is yet to explore (Hansda *et al*., 2008; Ojha *et al*., 2009; Reddy, 2010b). The existing genetic variation of economically important wild and domesticated silk insects need exploitation in commercial traits through effective breeding procedure (Sinha *et al*., 1994; Siddiqui, 1997; Nagaraju, 2002; Chatterjee and Mohandas, 2003; Verma *et al*., 2005; Moorthy *et al*., 2007; Reddy *et al*., 2010a). The genetic interaction through hybridization not only provides better parent heterosis (heterobeltiosis) but also contributes to improved silk quality due to the genetic diversity of the parental races involved in the breeding process (Verma *et al*., 2005; Reddy *et al*., 2008, 2009a). The fecundity, cocoon weight and shell weight showed higher co-heritability and significantly correlate with silk yield (Sinha *et al*., 2001; Reddy *et al*., 2009b). Moreover, the hybrids recorded better reeling presentation over pure races (Takabayashi *et al*., 1994) and shell weight and filament length correlated positively but filament thickness and length correlates negatively (Sekharappa *et al*., 1999). The fecundity, egg hatching, cocoon yield and shell weight together contribute to absolute silk yield (Sinha and Srivastava, 2004; Hansda *et al*., 2008). The optimal phenotypic expression of a genotype needs suitable climate and this relationship is called genotype and environment interaction (Srivastava *et al*., 2004; He and Wang, 2006; Reddy *et al*., 2009c). The gene is an endogenic factor and plays a major role, while the environment being the exogenic factor, it influences only the expressivity of genes to produce different phenotypes in different environments (Zhao *et al*., 2007). The extent of hybrid vigour in silk-related traits was found to vary under different temperatures (Srivastava *et al*., 2004; Kumar *et al*., 2008; Reddy *et al*., 2009d, 2010a). The variations in temperature, nutrient availability, feeding duration and crowding along with environmental stimuli influence the body plasticity (Davidowitz *et al*., 2004; Reddy *et al*., 2009c). The shortage of high yielding breeds in tasarculture requires utilization of available ecoraces for hybridization to improve the commercial traits. The aim of the present study was to combine the yield potential and survival consistency to achieve the best possible productivity through hybridization using three divergent ecoraces, i.e. the commercially exploited Daba from Jharkhand, the semi-domesticated Jata from Orissa and the wild ecorace Raily from Chhattisgarh states of India.

Materials and Methods

Rising and rearing of parental ecoraces and F_1 hybrids

Three parental ecoraces Daba, Jata and Raily of *A. mylitta* were initially reared during July - August (22~30ºC, 50~70% RH) of 2006 to 2008 at the field laboratory of the Central Tasar Research and Training Institute (CTR and TI), Ranchi (India) to rise the stocks of non-diapause destined seed cocoons. The fresh moths emerged during September of respective year from the above said cocoons preserved in the grainage house and were used to prepare disease free layings (Dfls) of F_1 hybrids of Jata × Daba, Raily × Daba and their reciprocals along with pure layings of three parents through selfing, following the integrated package of tasar seed cocoons preservation and seed production. Three parental ecoraces along with four F_1 hybrids, in total seven (n=7), were reared simultaneously in a randomized complete block design (RCBD) with three replications each during the commercial crop season of September-December (17~27ºC, 60~80% RH) during 2006 to 2008 on a *Terminalia tomentosa* (W and A) (Combretaceae) plantation at the field laboratory of CTR and TI following the integrated package of tasar silkworm rearing.

Parameters studied for commercial yield and calculation methods

The total larvae of one disease free laying (Dfl) of parents as well as F_1 hybrids were considered as one replication for recording observations. The commercial parameters like fertilized eggs per Dfl, larval span and single shell weight were calculated with 20 random samples, the silk yield was calculated multiplying the average (of 20 randomly selected cocoons/ Dfl) single shell weight by the number of cocoons harvested per Dfl, while the silk-related characters like length and denier of the silk filament were studied on a single cocoon basis (with 10 randomly selected cocoons). The mid parent heterosis (in %) of the F_1 hybrids was calculated over the parents of seed crop and commercial crop to assess the impact of hybrid vigour and season on phenotypic expression of commercial traits.

1. Silk yield (total or absolute) = average single shell weight of 20 randomly collected cocoons × number of cocoons harvested per Dfl
2. Mid parent heterosis (relative heterosis) = [(mean of F_1 generation - mean of two parental values) / mean of two parental values] × 100

Statistical analysis

The observations recorded on fertilized eggs, larval span, single shell weight, silk yield, silk filament length and denier were analysed using analysis of variance (ANOVA) to study the variation among treatments in seed and commercial crop (Kwanchai and Arturo, 1984). The statistical analysis was carried out in Windostat statistical software package (ver. 8.5, Windostat Services, Hyderabad, India).

Results

The data on performance levels of parental ecoraces Daba, Jata and Raily under *in-situ* habitation (Table 1) indicate variations in fertilized eggs, larval span, single shell weight, absolute silk yield, length and denier of silk filament as like their origin from different eco-geographic areas of the country, i.e. Jharkhand, Orissa, and Chhattisgarh. The commercially exploited Daba recorded higher number of average fertilized eggs (200), absolute silk yield (108.0 g) with lesser shell weight (1.80 g), shorter filament length (962 m), lesser larval span (38 days) and finer filament denier (10 d). The semi domesticated Jata and wild Raily ecoraces are superior in average shell weight (2.05 and 2.23 g) and filament length (1184 and 1385 m) while they show lesser fertilized eggs (130 and 110 no) and lower absolute silk yield (34.85 and 46.83 g) respectively, with longer larval span (39 and 40 days) and higher filament denier (12 and 13 d).

The analysis of variance results (Table 2) reveals significant differences in respect of egg, larva, cocoon and

Table 1. Performance levels of parental ecoraces (Daba, Jata and Raily) under *in-situ* habitation

Parameter	Daba		Jata		Raily	
	Range	Ave.	Range	Ave.	Range	Ave.
Fertilized eggs / Dfl (no.)	160 ~ 240	200	110 ~ 180	130	100 ~ 160	110
Larval span of crops (days)	29 ~ 48	38	30 ~ 45	39	30 ~ 50	40
Single shell weight (g)	1.25 ~ 2.36	1.80	1.60 ~ 2.34	2.05	1.97 ~ 2.82	2.23
Absolute silk yield/ laying (g)	62.5 ~ 177.0	108.0	24.0 ~ 44.5	34.85	35.5 ~ 70.5	46.83
Length of silk filament (m)	475 ~ 1240	962	840 ~ 1550	1184	570 ~ 1750	1385
Denier of silk filament (d)	9 ~ 11	10	11 ~ 13	12	12 ~ 14	13

Source: Sinha *et al*. (1994), Suryanarayana and Srivastava (2005), and Hansda *et al*. (2008).

Table 2. ANOVA results for economic traits of parental lines (six) and F_1 hybrids (four) for seed and commercial crop

Source of variation	d. f.	Fertilized eggs (no.)	Larval span (days)	Shell weight (g)	Silk yield (g)	Filament length (m)	Filament denier (d)
		MS	MS	MS	MS	MS	MS
Replicates	2	198.2	2.8	0.04	82.9	14281.6	0.17
Treatments	9	7059.7	72.6	0.38	6269.6	353645.2	3.32
Error	18	229.7	0.4	0.05	154.3	14144.5	0.39
F test (for treatment)		30.73**	183.21**	7.75**	40.62**	25.00**	8.42**
General mean		173.87	37.76	1.96	82.58	1248.87	12.14
SD		48.45	4.80	0.39	45.25	345.71	1.14
CV %		27.87	12.70	19.88	54.79	27.68	9.35

**, significant at 1% level; and MS, mean squares.

Table 3. ANOVA results for economic traits of parental lines (three) and F_1 hybrids (four) for commercial crop

Source of variation	d. f.	Fertilized eggs (no.)	Larval span (days)	Shell weight (g)	Silk yield (g)	Filament length (m)	Filament denier (d)
		MS	MS	MS	MS	MS	MS
Replicates	2	458.7	2.3	0.03	82.8	12322.7	0.001
Treatments	6	7694.6	11.2	0.25	8505.6	340959.4	3.04
Error	12	168.9	0.5	0.06	138.7	14106.9	0.45
F-test (for treatment)		45.55**	23.40**	4.22*	61.33**	24.17**	6.74**
General mean		175.14	40.65	2.12	87.48	1368.00	12.12
SD		49.55	1.97	0.34	51.41	334.64	1.09
CV %		28.29	4.84	15.94	58.77	24.46	8.97

*, significant at 5%; **, significant at 1%; and MS, mean squares.

silk related commercial characters for three parents each of seed and commercial crops and four F_1 hybrids of commercial crop rearing seasons. The results for commercial characters of the three parents and the four F_1 hybrids of the commercial crop rearing season also reveal the same trend except for single shell weight (Table 3). Significant differences of commercial characters between controls and treatments (T_1 to T_{10}) and also among treatments (T_4 to T_{10}) were found (Table 4).

The performance levels of egg, larvae, cocoon and silk characters in respect of parents of seed crop (T_1 to T_3), parents of commercial crop (T_4 to T_6) and F_1 hybrids of commercial crop (T_7 to T_{10}) seasons (Table 4) indicate better performance of parental races (T_4 to T_6) during the commercial crop season in all parameters except for silk yield of T_4 and T_6 over T_1 and T_3 of seed crop season. The Daba × Jata and its reciprocal Jata × Daba hybrids (T_7 and T_8) showed better performance in all the traits among F_1 hybrids. The Daba × Raily and its reciprocal Raily × Daba hybrids (T_9 and T_{10}) recorded better performance in shell weight and filament length and were inferior in fertilized eggs and silk yield, while the larval span was longer and

Table 4. Performance levels of parents of seed crop (T_1 to T_3) and commercial crop (T_4 to T_6) and F_1 hybrids (T_7 to T_{10}) of commercial crop (Mean ± SD)

Race/ Hybrid combination	Fertilized eggs (no.)	Larval span (days)	Shell weight (g)	Silk yield (g)	Filament length (m)	Filament denier (d)
Daba (T_1)	232 +/-4.58	31.0 +/-0.21	1.43 +/-0.12	96.2 +/-16.19	799 +/-149	10.61 +/-0.30
Jata (T_2)	149 +/-22.61	30.8 +/-0.46	1.63 +/-0.21	70.7 +/-5.13	1016 +/-137	12.59 +/-0.63
Raily (T_3)	132 +/-16.71	32.2 +/-1.00	1.75 +/-0.20	39.3 +/-16.39	1157 +/-60	13.65 +/-0.74
Daba (T_4)	243 +/-10.21	40.5 +/-0.83	1.70 +/-0.04	95.6 +/-11.26	880 +/-33	11.04 +/-0.58
Jata (T_5)	155 +/-23.16	41.5 +/-0.55	1.82 +/-0.21	85.6 +/-9.16	1249 +/-153	12.64 +/-0.51
Raily (T_6)	139 +/-21.22	41.9 +/-0.74	2.11 +/-0.15	36.7 +/-6.11	1257 +/-97	13.85 +/-0.80
Daba x Jata (T_7)	245 +/-13.11	38.1 +/-0.58	2.21 +/-0.30	162.2 +/-17.9	1790 +/-223	11.98 +/-0.43
Jata x Daba (T_8)	183 +/-7.94	38.1 +/-0.89	2.09 +/-0.24	152.3 +/-17.2	1744 +/-84	12.32 +/-0.30
Daba x Raily (T_9)	137 +/-6.11	41.2 +/-1.36	2.45 +/-0.35	44.9 +/-4.81	1109 +/-33	12.18 +/-0.86
Raily x Daba (T_{10})	124 +/-10.44	43.2 +/-0.83	2.47 +/-0.21	35.0 +/-5.23	1546 +/-69	10.86 +/-0.69
LSD at 5% (For comparison of treatment means T_1 to T_{10})	26.00	1.08	0.38	21.31	204.02	1.08
(For comparison of treatment means T_4 to T_{10} excluding control)	23.12	1.23	0.44	20.95	211.31	1.19

Table 5. Levels of mid parent (relative) heterosis percentage of F_1 hybrids (T_7 to T_{10}) (+ or - heterosis percentage over mid parents of seed and commercial crops)

Hybrid combination	Fertilized eggs (no.)	Larval span (days)	Shell weight (g)	Silk yield (g)	Filament length (m)	Filament denier (d)
Daba x Jata (T_7)	+28.6 +23.1	+23.3 -07.1	+44.4 +25.6	+94.5 +79.0	+97.2 +68.1	+03.30 +01.20
Jata x Daba (T_8)	-03.9 -08.0	+23.3 -07.1	+36.6 +18.8	+82.6 +68.1	+92.2 +63.8	+06.20 +04.10
Daba x Raily (T_9)	-24.7 -28.3	+30.4 =0.00	+54.1 +28.3	-33.7 -32.1	+13.4 +03.8	+0.41 -02.1
Raily x Daba (T_{10})	-31.9 -35.1	+36.7 +04.9	+55.3 +29.3	-48.3 -47.0	+58.1 +44.7	-10.5 -12.7

filament denier was less in T_9 and least in T_{10}.

The percentage heterosis of F_1 hybrids in respect of egg, larvae, cocoon and silk characters over the mid parent value of seed and commercial crops (Table 5) revealed better positive heterosis by Daba × Jata hybrid and its reciprocal Jata × Daba (T_7 and T_8) over mid parent of seed and commercial crops in all parameters with marginally higher filament denier by T_7 and T_8, except for fertilized eggs by T_8. However, both hybrids recorded shorter larval span over the parents of commercial crop and hence showed negative in heterosis. The Daba × Raily and its reciprocal Raily × Daba hybrids (T_9 and T_{10}) revealed positive mid parent heterosis over the parents of both crop seasons only in shell weight and filament length. However, they have shown finer filament denier and longer larval span and hence recorded negative and positive in heterosis, respectively, for filament denier and larval span. Yet, both T_9 and T_{10} hybrids of Daba and Raily showed negative heterosis in respect of fertilised eggs and silk yield over the parents of both crop seasons.

Discussion

Achieving breeding objectives in silkworms require precise selection, starting from the initial choice of parents, meticulous progeny testing and matching ecological and nutritive conditions (Nagaraju, 2002). The differing performance levels of parental ecoraces clearly indicate their distinctiveness due to their origin from different Indian ecozones with feasible genetic diversity (Sinha *et al*., 1994; Siddiqui, 1997; Suryanarayana and Srivastava, 2005). The higher number of fertilized eggs in the commercially exploited Daba ecorace with shorter larval span, highest silk yield and finer filament denier in spite of lower shell weight prove its commercial superiority and economic viability. The semi-domesticated Jata and the wild Raily ecoraces, in spite of having better shell weight and longer filament length, require additional breeding efforts because of their low egg fertility, lesser silk yield and comparatively longer larval span (Sinha *et al*., 2001; Sinha and Srivastava, 2004; Suryanarayana and Srivastava, 2005; Hansda *et al*., 2008; Reddy *et al*., 2008, 2009c, 2010b). The mixing of superior and advantageous economic characters of commercially exploited semi-domesticated and wild ecoraces for hybrid vigour (Siddiqui, 1997; Moorthy *et al*., 2007; Reddy *et al*., 2009a) in economic traits at F_1 level for a industrially sustainable tasar breed made to choose the Daba, Jata and Raily ecoraces of *A. mylitta* as parents.

The significant phenotypic and performance differences among parental ecoraces (Daba, Jata and Raily), irrespective of their natural habitat and rearing seasons, indicate the existence of genetic divergence among them. Further, the varied performances among parents and F_1 hybrids under seed and commercial crop seasons illustrates the heterosis potential, however, with the impact of environment on phenotypic expression of a recombinant hybrid genotype. The better performance of parents (T_4 to T_6) of the commercial crop over the parents (T_1 to T_3) of the seed crop season indicates the influence of changed rearing conditions on the performance of a genotype (Srivastava *et al*., 2004; Zhao *et al*., 2007; Kumar *et al*., 2008; Reddy *et al*., 2010a). To achieve optimal breeding goals, the rised hybrids need to be tested simultaneously with their parents under suitable environmental conditions. The higher performance differences among parents and F_1 hybrids (T_4 to T_{10}) in spite of their unvarying rearing environment (commercial crop season) affirm the clear hybrid vigour on egg, larva, cocoon and silk related economic traits (Takabayashi *et al*., 1994; Nagaraju, 2002; Verma *et al*., 2005; Reddy *et al.,* 2009a, 2010a).

The tasarculture is an outdoor practice and its performance depends on the rearing season. While bivoltine tasar silkworm exhibits varied cocoon characters during the seed (July - August) and the commercial crop (September - December) seasons of the year due to interaction among seasonal variations, larval duration (Zhao *et al*., 2007; Reddy *et al*., 2009d), rearing environment, feed quality (Davidowitz *et al*., 2004; He and Wang, 2006; Reddy *et al*., 2009c) and the diapause and non-diapause compatibility of generation. The tasar silkworm is characterized by a wide variability in yield and developmental traits, which have been proven through conventional genetic analysis to be of polygenic nature (Chatterjee and Mohandas, 2003), correlates the varied performances of their economic traits. The shorter larval span of the seed crop led to thin cocoon shell, non-diapausing cocoons, simultaneous and easy moth emergence followed by egg laying, while the subsequent commercial crop with longer larval span, thicker cocoon shell with prolonged pupal diapause of 6~7 months. This also underlines the role of the environment in exhibiting the phenotypic characters of a genotype forecasting the environmental change ahead and hence the comparison has been made among the parents of both crop seasons along with F_1 hybrids of commercial crop season. This nullifies the environment associated elevated performance in traits of parental races, when compared with the performance of F_1 hybrids and helps assessing the actual extent of hybrid vigour on economic traits.

The improvements in respect of egg fertility, shell weight, filament length in parents of the commercial crop season, i.e. T_4 to T_6, over their respective parents of the seed crop season and also the silk yield in T_5 (Jata) indicate the role of the environment in varied phenotypic expression of the ecoraces (Hansda *et al*., 2008; Kumar *et al*., 2008; Reddy *et al*., 2009c) and the combined impact of improved egg, larva and cocoon traits (Sinha and Srivastava, 2004). However, the silk yields in T_4 (Daba) and T_6 (Raily) were reduced marginally in the commercial crop season in spite of the improved egg fertility, shell weight and filament length, which was possibly due to low effective rate of rearing and cocoon yields besides the racial characteristic performances under changed environment. Yet, the extended larval span and increased filament denier are the commercially weaker points which indicate the preparation of the insect for diapause by storing more food reserves and thick cocoon shell. While comparing the performances on mid parent heterosis of F_1 hybrids, the Daba x Jata (T_7) showed improvement over the parents of seed and commercial crop seasons with strong hybrid vigour through an elevated leap in silk yield and filament length (Siddiqui, 1997; Sekharappa *et al*., 1999), indicating its industrial prospective. The positive heterosis in T_7 (Daba × Jata) over the parents of the commercial crop season was higher in all tested traits except for filament denier, indicating distinct hybrid vigour on many economic traits (Nagaraju, 2002; Moorthy *et al*., 2007; Reddy *et al*., 2009d,2010b). Though, there is increase in larval span and filament denier, it found less than their respective parents of corresponding rearing season and the proportionate increase of silk yield and filament length are far higher. But, the decrease in the larval span by these hybrids in commercial crop over their mid parent is another positive aspect of commercial importance. The reciprocal F_1 hybrid Jata × Daba (T_8) could also perform next to T_7, in spite of decrease in egg fertility and increase in filament thickness, superseding its parents in overall performance competing as another potential commercial breed option. The F_1 hybrid, Daba × Raily and its reciprocal, Raily × Daba (T_9 and T_{10}) have shown positive heterosis in shell weight, filament length and additionally in filament denier by T_{10}, but were negative in very important economic trait, the silk yield. These results indicate hybrid weakness and trait associated negative heterosis (Sinha *et al*., 1994; Siddiqui, 1997; Nagaraju, 2002; Verma *et al*., 2005; Reddy *et al*., 2009a, 2010b) of T_9 and T_{10} and coincide with restricted performance of one of its parental ecorace i.e. Raily under *ex-situ* conditions. This might also be due to decreased fertilized eggs, longer larval span in addition to non-acclimatization to changed rearing environment and food plant by Raily ecorace; as it survives better under natural (*in-situ*) habitat on food plant, *Shorea robusta*. The major share of country's tasar raw silk production is from natural grown Raily cocoons, although indicate its potential, but was from its natural habitat only.

The study infers that, the F_1 hybrids, Daba × Jata (T_7) and Jata × Daba (T_8) posses maximum hybrid vigour on economic traits and hence the generation of parental cocoons in seed crop season to produce Dfls (seed) as F_1 hybrids and rearing them during commercial crop season can optimize their phenotypic expressiveness contributing for better silk yield and quality for the commercial sustenance of tasar silk industry.

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